



Strong fish assemblage patterns persist over sixteen years in a warming marine park, even with tropical shifts

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ABSTRACT

Spatial conservation plans representing existing patterns of biodiversity in Marine Protected Areas (MPAs) should be robust to changes over 10 to 20 years, a temporal scale over which MPA plans are often retained. Using data from MPAs where changes have been detected due to ocean warming, can help inform discussion on how to increase temporal robustness in planning. Our aim was to determine how well fish assemblage patterns, used to develop a Habitat Classification System (HCS) as a coarse biodiversity surrogate in MPA planning, persisted over a 16 year timeframe in a warming region (east coast subtropics) of Australia. We analysed persistence/change in fish assemblage patterns in the Solitary Islands Marine Park (SIMP) where species shifts and habitat changes associated with ocean warming have been detected. Fish relative abundance was recorded at 12 sites over 16 years (2001–2017) using roving timed counts. Strong cross-shelf patterns were maintained over that 16 year period, which included some large-scale disturbances (destructive storms, 2016 mass coral bleaching event). Overall persistence in these broad assemblage patterns suggest a well-designed HCS can be a robust tool for coarsely representing biodiversity patterns in a warming world at decadal scales. ‘Tropicalisation’ was detected in some categories, suggesting additional planning strategies are needed within those and beyond decadal plans.

1. Introduction

Representation of biodiversity in a spatial management framework is an important strategy for Marine Protected Areas (MPAs) globally (e.g. Convention on Biological Diversity Aichi Target 11) and at a more localised spatial extent (e.g. NSW Marine Estate Management Authority, 2017). This strategy requires good knowledge of patterns of various components of biodiversity for effective spatial planning in multiple use MPAs. Yet this knowledge is often constrained due to the cost and difficulty in obtaining data across broad spatial extents in the marine environment. In the absence of full knowledge of biotic patterns at the spatial extent of a marine park, surrogates are often used (Dixon-Bridges et al., 2014; Grantham et al., 2010; Malcolm et al., 2012). Surrogates generally integrate biotic pattern with physical and environmental or biological attributes (e.g. depth, habitat characteristics, dominant benthos) that are more readily measured at the desired scale (Ferrier, 2002). Surrogates, whether they are environmental, physical, or taxonomic, require testing over space and time to assess their effectiveness at reflecting the distribution of some feature of biodiversity (Grantham et al., 2010) in relation to their intended management

objective (Hunter et al., 2016; Turnbull et al., 2018).

Habitat types have long been used as a surrogate for biodiversity patterns in MPA planning to provide guidance in designing the spatial arrangement of zones (Malcolm et al., 2010b; Rees et al., 2013; Stevens and Connolly, 2004; Ward et al., 1999). Integrating seafloor habitat mapping and biotic assemblage patterns can improve spatial conservation planning where biotic and physical patterns strongly correlate and where effective remote mapping (i.e. swath acoustic mapping, aerial based laser mapping, satellite imagery) has been undertaken (Ferrier, 2002; Malcolm et al., 2016). One integrated approach includes developing a Habitat Classification System (HCS) where habitat categories have significantly dissimilar biotic assemblages (Malcolm et al., 2011b). Habitat classification is a coarse surrogate, suitable for guiding selection among habitat categories but not selection within a category. This constraint can be addressed by utilising additional finer spatial extent and resolution methods within categories, such as species distribution modelling, and by incorporating local knowledge (Ferrari et al., 2018a).

Spatial management also occurs in a temporal context. Often considerable cost, time, logistics, and community effort are expended

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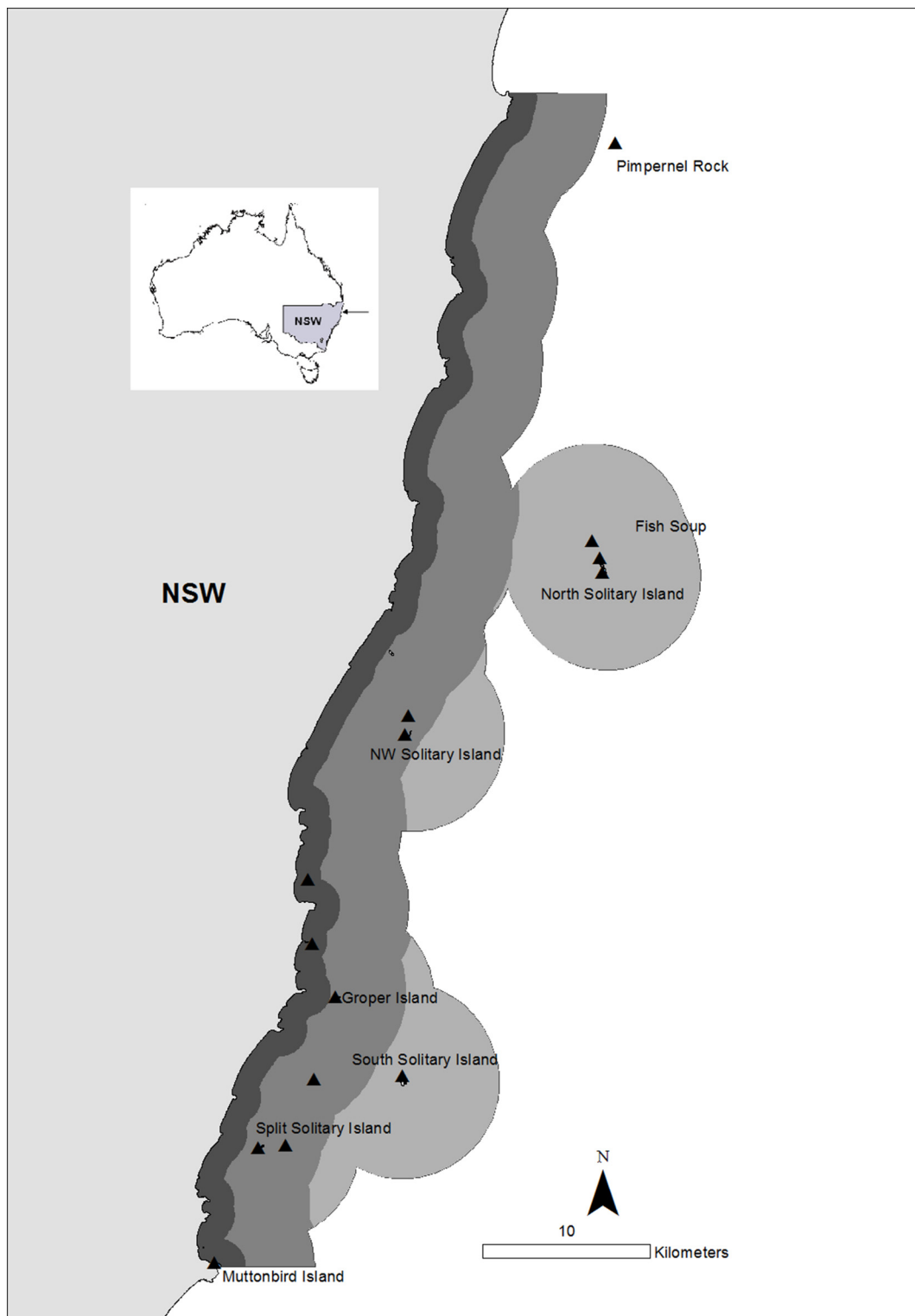


Fig. 1. Map of sites. Dark grey = inshore waters; mid grey = mid waters; light grey = offshore waters, in the Solitary Islands Marine Park. Very light grey = land, New South Wales (NSW).

establishing an MPA or, in the case of multiple use marine parks, modifying individual management plans governing them (Banks and Skilleter, 2010). Therefore once established, unless setup as a dynamic MPA, changing the spatial management framework within a multiple use MPA is not something undertaken lightly, without there being good rationale or legislative requirement. This is especially the case in relation to ‘no take’ areas, which exclude extractive activity. Often

management plans are in place at least over the decadal temporal scale and decadal timeframes are often required for desired biological responses to occur (Babcock et al., 2010; Edgar et al., 2009, 2014; Ferrari et al., 2018c; McClanahan and Humphries, 2012). However, additional to temporal variability at a range of scales (e.g. days, moon cycles, seasons, years, decades), temporal changes in the environment and biotic distributions are occurring regionally and globally associated

with ocean warming (Booth et al., 2011; Hughes et al., 2017; Vergés et al., 2016; Wernberg et al., 2016). Thus, there is a need for MPAs, particularly ‘no take’ areas to consider both existing and future biotic patterns to successfully represent and preserve/conservate biodiversity (Magris et al., 2015; Makino et al., 2014; Pecl et al., 2017), including the influence of discrete extreme events (Jones et al., 2016; Galaiduk et al., 2017).

Changes associated with major perturbations can be somewhat ameliorated by retention of strong physical or environmental features, which may help to maintain persistence of biotic patterns (Emslie et al., 2014). For example, on the Great Barrier Reef, Australia, there are strong cross-shelf patterns in benthic communities and functional groupings of fishes (Hoey and Bellwood, 2008; Wismer et al., 2009) influenced by terrestrial river inputs (Fabricius, 2005). The current spatial configuration of reefs, coastline and rivers on the GBR is unlikely to change at decadal scales, but has changed at geological time-scales with sea level variation. The East Australian Current (EAC) is a strong, warm, western boundary current that also influences cross-shelf patterns on the GBR and New South Wales (NSW) as it flows southwards along the eastern Australian coast (Ridgway and Dunn, 2003; Suthers et al., 2010) transporting tropical larvae. The EAC combined with cooler counter-currents flowing northwards and upwelling generated by the EAC itself (Cresswell et al., 1983; Marchesiello and Middleton, 2000; Roughan and Middleton, 2002, 2004), facilitate the establishment of a tropical-subtropical-temperate overlap in northern NSW that is reflected in the community composition and spatial distribution of the regional biota (Booth et al., 2007; Harriott et al., 1994; Harrison and Smith, 2012; Malcolm et al., 2010a). Even though the EAC is predicted to strengthen (Poloczanska et al., 2007), penetrate further southwards (Ridgway, 2007), and is warming southeast Australia 2–3 times faster than global mean surface ocean shift (Wu et al., 2012); features such as gradients in the occurrence and strength of the EAC from inshore to offshore in northern NSW, are likely to be persistent. This includes flowing strongly past the Solitary Islands Marine Park (SIMP) in northern NSW, immediately upstream of the most frequent separation point (~32° S) of the EAC from the Australian coast (Suthers et al., 2010).

The SIMP, established in 1991, includes a series of islands ranging up to 12 km from the mainland coast, creating areas of shallow rocky reef (< 25 m depth) from inshore to offshore. Associated with shallow habitat cross-shelf and the stronger influence of the EAC offshore, there are strong cross-shelf patterns in macro-algae, scleractinian corals, molluscs, and fish assemblages (Harriott et al., 1994; Harrison and Smith, 2012; Malcolm et al., 2010a; Veron et al., 1974) driven by differences in the distribution of tropical, subtropical, and temperate species. The objective of this study was to examine temporal persistence of cross-shelf patterns in assemblages of reef fishes in the SIMP over a period of 16 years. The aim to assess whether the key features used to develop a Habitat Classification System for planning spatial representation of biodiversity patterns in ‘no take’ areas in this marine park, have been maintained over that time-frame despite acute and chronic disturbances.

2. Materials and methods

2.1. Survey design

Twelve reef sites were surveyed cross-shelf in the Solitary Islands Marine Park (SIMP) in northern New South Wales (NSW), Australia (Fig. 1). Sites were in shallow (< 25 m depth) reefs and distributed among Habitat Classification System (HCS) categories developed for conservation planning in the SIMP (Malcolm et al., 2010b): three sites inshore (< 1.5 km from shore); six sites mid-shelf (1.5–6 km from shore); and three sites offshore (> 6 km from shore). Of the six mid-shelf sites, three were on reef adjacent to islands and three were on fully submerged reef. These four categories (1: inshore, 2: mid island, 3: mid

submerged, 4: offshore) comprise the factor ‘Position’. These sites were surveyed eight times over a 16 year period (2001 to 2017) during the Austral autumn. An additional two sites (Pimpnel Rock, Fish Soup), locally recognised as having important conservation values and unique assemblages (Malcolm et al., 2010a), and therefore considered as ‘special’ were also sporadically surveyed five times over the 16 year duration.

Period was also a main factor in the survey design. Sampling conducted during the first five years of this study (2001 to 2005) were categorised as period 1 and surveys during the last five years of the study (2013 to 2017) were categorised as period 2. We examined period as a factor due to eight years separating the two clusters of sampling, which were both within a five year period. Additionally, there was a greater intensity of environmental perturbation over the second period, commencing with a series of powerful East Coast Lows (generating destructive storm swell events) between 2009 and 2017 (Vergés et al., 2016) and including a mass coral bleaching event in 2016, which strongly affected some subtropical coral species but not others (Hughes et al., 2017).

2.2. Fish and physical-environmental data

2.2.1. Fish data

A roving 30-min timed count was conducted at each site during which all species observed were recorded and given a relative abundance rating using a log₅ estimate (Kingsford, 1998; Malcolm et al., 2010b). Due to the geomorphology of this area, there is a greater depth-range at offshore sites compared with inshore sites, which could influence spatial pattern through differences in physical habitat and environmental processes. However, the potential loss of information on the influence of depth on reef fish assemblages was a recognised and accepted consequence of this sampling approach for the objective of examining cross-shelf persistence in patterns. Additionally, although there is a strong influence of depth between shallow (0–25 m), mid-depth (25–50 m) and deeper (50–75 m) reefs in the area (Malcolm et al., 2011b), depth has been found to have little influence on reef fish assemblages within the mid-depth range (Ferrari et al., 2018b). Thus, within each depth category, cross-shelf patterns should be stronger than the influence of depth, and all sites in this study were in the shallow depth category (0–25 m). At each site, the survey began near the deepest part of the reef and proceeded in a zig-zag pattern to shallower depths; inshore from about 5 to 15 m and offshore from about 5 to 20 m.

A consistent, slow rate-of-swim was used to cover a similar area during each survey (approximately 200 × 10 m). This involved keeping a mental tally of the approximate number of individuals for each species, and sequentially marking off each abundance category as it was reached (Malcolm et al., 2010b). Surveys were conducted during daylight hours (0900–1600 h) with the same observer (HM) conducting all counts over the 16 year period. Log₅ abundance scores were: 1 = 1 fish; 2 = 2–5; 3 = 6–25; 4 = 26–125; 5 = 126–625; 6 = 626–3125; 7 > 3125.

Although all species observed were recorded, the focus of the survey was on non-cryptic species. Cryptic species were included when sighted, but methods were not tailored towards searching for cryptic individuals (Ackerman and Bellwood, 2000). New recruits and young-of-the-year were not included to reduce potential seasonal confounding and to exclude species that may settle but not survive winter sea-temperatures in this area (Booth et al., 2007, 2011; Figueira and Booth, 2010).

2.2.2. Physical-environmental data

Additional to position (categorical), period (categorical) and year (continuous), a range of continuous physical and environmental variables (e.g. sea temperature, depth, distance and latitude) were determined to help interpret findings through modelling. Sea temperature

was monitored at two inshore, two mid island and three offshore sites during the duration of this study using logging thermistors (Malcolm et al., 2011a) to indicate annual averages, annual minima and annual maxima by position and survey year. Loggers were deployed for up to 12 months and recorded sea temperature every 30 min. Sites were in approximately 10 m depth of water, with thermistors attached to the seafloor. Onset 32 K TidbiT loggers (Onset Computer Corporation, MA, USA) were used from 2001 to 2006. Dataflow Odyssey loggers (Dataflow Systems Ltd., New Zealand) were used from 2006 to 2011, Reefnet Sensus loggers from 2011 to 2014, and from 2011 to 2017 Onset Hobo Pro V2 loggers. Data were averaged across the two sites per position for each 30 min, as in some years data was missing from one site due to logger failure. When combined, there was full 30 min data coverage offshore and mid, but there was no data for 2001 inshore, all other years had data for inshore, mid and offshore.

Other physical data considered likely to influence patterns were either obtained in situ during field surveys (minimum depth, maximum depth, depth range, latitude) or determined using GIS (distance from shore).

2.3. Data analysis

2.3.1. Multivariate data analyses

Patterns in fish assemblages were initially visualised with non-metric multi-dimensional scaling (nMDS) ordinations using PRIMER v7 (Clarke et al., 2014). Species accumulation plots overall and by position were used to examine whether new species were being observed each year of survey and if there were trends in the number of species observed over time.

Permutational multivariate analyses of variance using PERMANOVA+ for PRIMER v 7.0 (Anderson et al., 2008) were used to compare multivariate fish assemblage structure between the 4 main positions of interest (inshore, mid submerged, mid island, offshore) for the two main fixed factors of interest: 'position' and 'period' (2 levels: 2001–2005 and 2013–2017) and their interaction. Analyses included a third factor 'year' which was nested within period (Anderson, 2001). The timed count at each site was the replicate (position $n = 4$, period $n = 2$, position $\times$ period = 8, year = 8). PERMANOVA analyses were run using 9999 iterations. Separate PERMANOVA analyses compared assemblage structure between the two 'special' sites and the four positions (special site/position $n = 6$). Bray-Curtis similarity matrices were used without transformation given these are already log5 estimates. Assemblage composition (Beta diversity) was also compared using PERMANOVA with the dissimilarity matrix generated using the Jaccard measure on presence/absence of species (Anderson et al., 2006, 2011). This second analysis allows for a comparison in the compositional variability between the 4 main positions of interest across time ('position' and 'period'). Estimates of community compositional variation such as Beta diversity can be used to detect more rapid changes compared with mean changes in abundances (Thrush et al., 2010; Whittaker, 1972). Multivariate dispersion was compared among positions using PERMDISP in PRIMER v7 (Anderson et al., 2008) to consider multivariate heterogeneity for untransformed data and was found to be non-significant.

As well as the overall assemblage, analyses were done on groups, including: families (Labridae, Pomacentridae, Chaetodontidae); ecoregion groups (subtropical, tropical, temperate species); subtropical SW Pacific endemic species; and trophic functional groups (higher carnivores, invertivores, herbivores, planktivores) to further inform findings (Supplementary material 1). Labrids and Pomacentrids were assessed as these are the two most speciose families and combined are a good surrogate for overall assemblage patterns (Malcolm and Smith, 2010). Chaetodontids are predominantly tropical in ecoregional affiliation and can therefore reflect a strong tropical signal. Categorisation for each species into functional and ecoregion groupings was based on a combination of FishBase descriptions (<https://www.fishbase.de/search.php>), FishMap - Atlas of Living Australia distribution maps (<https://fish.ala.org.au/>), Reef Life Survey distribution maps (<https://reeflifesurvey.com/species/search.php>), and Australian fish identification books (Kuitert, 2000; Randall et al., 1997).

2.3.2. Fish abundance analyses

The relationship between environmental predictors and fish abundance was further investigated using eight univariate models: one for the overall fish abundance, and seven for each functional group used in the multivariate analyses (Labridae, Pomacentridae, Chaetodontidae, tropicals, subtropicals, temperates, and subtropical species endemic to the Southwest Pacific, see SM 1). When data exploration detected high correlation (Pearson $r > 0.75$) between some explanatory variables (i.e. maximum annual temperature and average annual temperature); we selected only one of the correlated variables to be included in the models (i.e. average annual temperature). The selection of explanatory variables to be included was informed by the correlation coefficient and the ecological importance of each explanatory variable to fish abundance. None of the explanatory variables included in a model were highly correlated (Dormann et al., 2013). Thus, all models tested the influence of two categorical explanatory variables and their interaction (position, period), and four continuous explanatory variables (distance from mainland coast, latitude, minimum depth, average annual temperature). Outliers were detected and removed for two fish groups during data exploration: Chaetodontidae (10 outliers of 106 data points) and temperate fish species (3 outliers of 106 data points). Data exploration also investigated the distribution of response variables to inform model type and distribution, several distributions were tested during the modelling process (i.e. Poisson and negative binomial).

We used general, generalized and zero inflated hierarchical models (GLM/GLMM/GLMMADMB) in R packages 'lme4' (Bates et al., 2013), 'mass' (Venables and Ripley, 2002) and 'glmmadmb' (Fournier et al., 2012; Kristensen et al., 2016). The choice and type of model was informed by the need to account for 1) random effect of year, and 2) potential zero inflated or over dispersed data. Year nested within period, year and period (each separately) were tested as random effects in the original models; if improvement of model fit from including random effects was not significant ($p > 0.05$) these were removed from the models. Models were simplified using backward selection following the parsimony principle, and tested using χ^2 -test on likelihood ratios and AIC to determine the best model (AIC only for GLMs). Assumptions of homoscedasticity, over dispersion and normality (when relevant) were checked using residual plots (package 'graphics') (R-Core-Team, 2013) for all final models (Bates et al., 2013; Zuur et al., 2009, 2010).

3. Results

3.1. General species occurrence and abundance, species accumulation and assemblage patterns

A total of 279 reef fish species were recorded at the 12 sites over the 16 year period (SM 1). The initial survey year recorded a high proportion of these (58%), although by the end of the study (from 96 thirty-minute timed counts at the 12 sites) the species accumulation curve had not reached asymptote with 6 additional species recorded in 2017. An additional 17 species were also only recorded from the two 'special' sites during the study.

Overall, between 153 and 177 species were recorded each year, with the lowest numbers in 2003 and the highest in 2016. However, this number fluctuated between years, with 2015 (154 species recorded) similar to 2003. Similar numbers of species were detected in each of the eight years for the inshore position, the most stable of the four positions in terms of species occurrence (Fig. 2). The mid island position also remained relatively similar between years except for increasing numbers towards the end of the study, especially 2017.

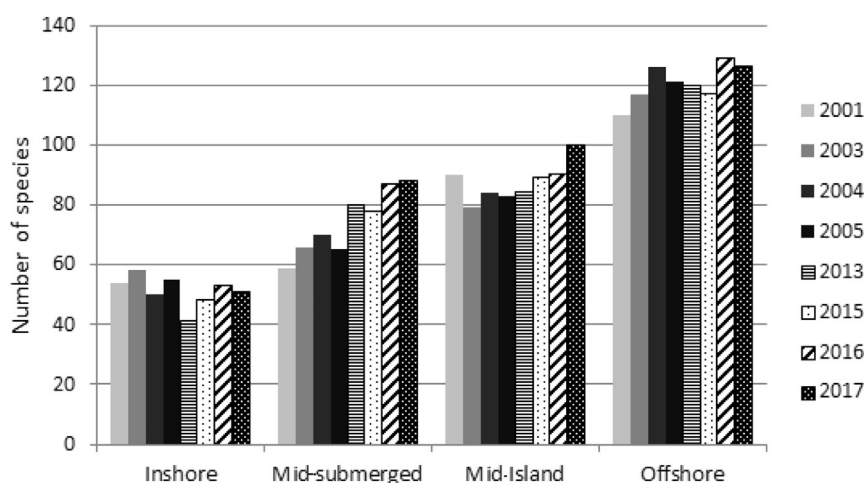


Fig. 2. Number of fish species recorded by position and by year.

Contrary to these more stable patterns, offshore and mid submerged reefs showed a general trend of increasing numbers over time. Offshore, the number of species increased from 2001 to 2017 with the highest number in 2016 ($n = 129$), but 2004 was also high ($n = 126$). The strongest pattern of increase was on the mid submerged reefs, which includes reefs where kelp has disappeared over the duration of this study.

The overall fish assemblage pattern, by position and period, visually persisted over the study period (Fig. 3). Inshore sites, mid sites, and offshore sites formed distinct clusters. Although mid island and mid submerged sites were more similar to each other than to inshore and offshore sites, visually there was some separation between them. Although remaining clustered for the full study, there was also an

apparent and consistent shift within all four positions from period 1 to period 2 towards the right of the MDS plot. Given the more temperate inshore sites are on the left side and the more tropical offshore on the right, this suggests a shift towards a more tropical system overall, at the marine park spatial extent. The two 'special' sites (Pimpernel Rock, Fish Soup), which are both positioned offshore, remained in two discrete clusters throughout the study and likewise showed a shift towards the right in period 2 within each cluster (Fig. 3).

3.2. Assemblage structure and composition comparisons between positions and between periods for overall assemblage

PERMANOVA revealed that the overall assemblage structure

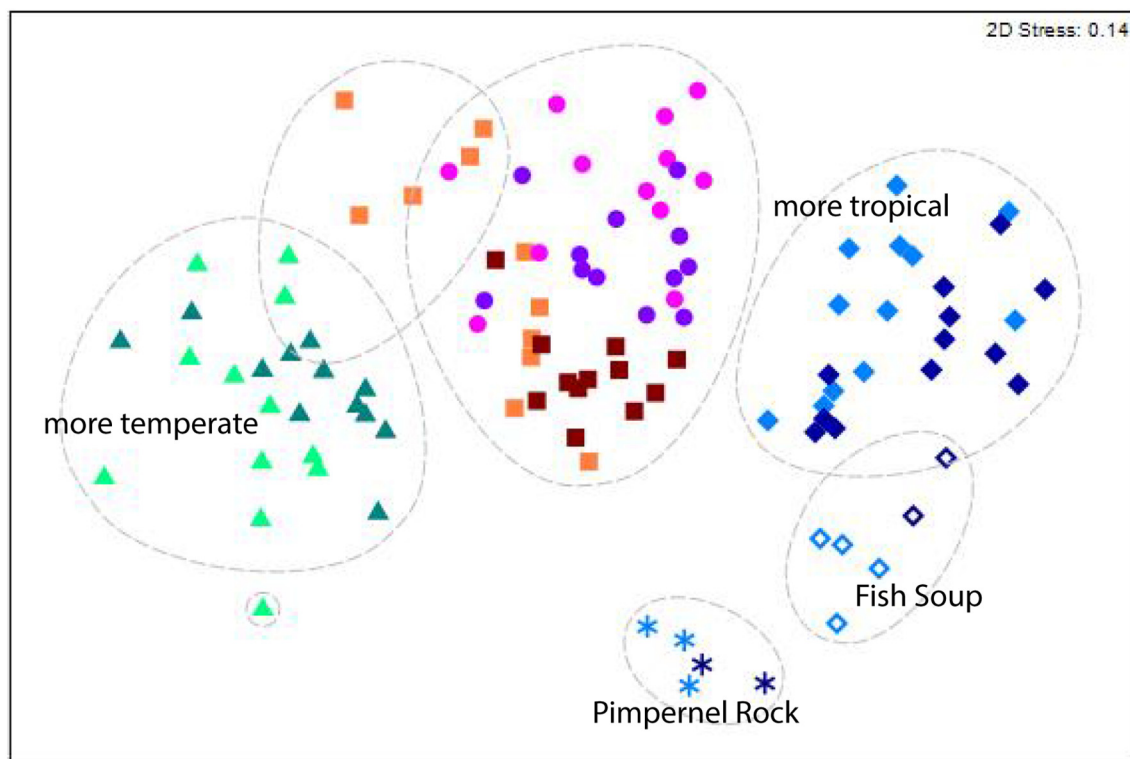


Fig. 3. 30 minute roving timed Log5 abundance counts at 14 sites over a 16 year period. Green triangles = inshore, orange/brown squares = mid-submerged, pink/purple circles = mid-islands, blue diamonds = offshore. Lighter shade = 2001 to 2005, darker shade = 2013 to 2017. Blue asterisk = Pimpernel Rock 'special' site. Blue hollow diamond = Fish Soup 'special' site. $n = 296$ spp. Dashed lines = 50% dissimilarity. Stress = 0.14. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Pairwise comparisons between the four main positions overall. Pairwise comparisons between period 1 (2001 to 2005) and 2 (2013 to 2017) within each position. Bold P(permutation) values are statistically significant at $\alpha < 0.05$.

Between positions	P (perm)
Inshore, mid submerged	0.0001
Inshore, mid island	0.0004
Inshore, offshore	0.0002
Mid submerged, mid island	0.0021
Mid submerged, offshore	0.0002
Mid island, offshore	0.0003
Between periods (1 and 2)	P (perm)
Inshore	0.3686
Mid submerged	0.0062
Mid island	0.0579
Offshore	0.0316

significantly differed by position ($P = 0.0001$) and period ($P = 0.0072$) and their interaction ($P = 0.0032$). From pairwise comparisons all four position categories (inshore, mid island, mid submerged, offshore) significantly differed from each other overall (Table 1) and within each period. Significant difference between periods was predominantly driven by changes in offshore and mid submerged reefs (Table 1) concordant with the pattern associated with number of species recorded each year by position. Although overall the number of species recorded in the mid island category was similar in period 1 and period 2, there was an apparent increase in 2017 (Fig. 2, Table 1).

Nested within periods, there were significant differences between years ($P = 0.0244$) during the second period (2013 to 2017). This was driven by 2013 differing in pairwise comparisons with 2015, 2016, and 2017 ($P = 0.0378$, 0.0342 , 0.009 , respectively). These latter three years did not significantly differ. Likewise pairwise comparisons between 2001, 2003, 2004 and 2005 did not significantly differ.

When the two ‘special’ sites were included in analyses these significantly differed from each other and from the four positions (overall ranging between $p = 0.02$ and $p = 0.0005$ for all pairwise combinations). As suggested by the MDS and confirmed using PERMANOVA, these distinct ‘special’ sites remained distinct over the survey period (all p values for all combinations were < 0.02).

When comparing Beta biodiversity using Jaccard dissimilarity on presence/absence data, PERMANOVA revealed that the assemblage composition significantly differed by position ($P = 0.0001$) but not period ($P = 0.1328$). From pairwise comparisons all four position categories (inshore, mid island, mid submerged, offshore) significantly differed from each other.

3.3. Assemblage structure comparisons between positions and between periods for fish groups

From PERMANOVA, all groups that were examined (Labrids, Pomacentrids, Chaetodontids, tropical species, subtropical species, temperate species, southwest Pacific subtropical endemics, higher carnivores, invertivores, herbivores, and planktivores) showed very strong significant differences (Table 2) between positions ($P < 0.001$). Period also significantly differed for all groups except Chaetodontids, but not as strongly (Table 2). From pairwise comparisons between the four ‘positions’ (inshore, mid-island, mid-submerged, offshore), all four positions significantly differed for every group except Chaetodontids and invertivores. For these two groups all positions significantly differed except for mid-island and mid-submerged. Pairwise comparisons were not undertaken for period as a main significant result because period only had 2 levels, which means that if period was significant, period 1 was significantly different from period 2 (Table 2).

The interaction between position and period was significant for Labrids, Pomacentrids, tropical species, temperate species, herbivores, invertivores and planktivores. Fish abundance changed between periods for these groups but in different ways depending on the position. For example, average abundance of Labrids increased at all four positions from period 1 to period 2 but most-strongly offshore and at mid islands relative to the other two positions. Interestingly, the number of labrid species detected decreased slightly from period 1 to period 2 at all locations (inshore 17 to 15; mid subtidal 31 to 26; offshore 39 to 36) except mid islands which remained similar (28 to 29).

Overall, a similar visual ordination (MDS) pattern to that of the overall assemblage was found for all the groups (Supplementary material 1), with some separation between the different positions. For all 11 groups there was complete separation between inshore and offshore sites. For some groups (Labrids, tropical spp., temperate spp., invertivores) mid sites fully separated from inshore and offshore, whereas for others there was some overlap between mid with both inshore and offshore (Chaetodontids, subtropical spp., SW Pacific subtropical endemics) or just between mid and offshore (Pomacentrids and herbivores). For some groups there was strong separation between mid-island and mid-submerged sites (Pomacentrids, tropical species). For example, Pomacentridae more strongly differed between mid-island and mid-submerged sites than Labridae. Chaetodontids were predominantly only recorded offshore and at mid islands, which clustered separately. Chaetodontids were detected at three mid submerged sites in period 1 which increased to seven in period 2. For higher carnivores, the ordination stress was too high > 0.21 , to visualise in 2 dimensions.

3.4. Cross shelf in situ sea temperature patterns 2001 to 2017

Sea temperature showed considerable variation among years during the period 2002 to 2017, with 2016 having the warmest temperatures overall and the only year temperatures exceeding 27°C in the inshore and mid island positions (Fig. 4, Table 3, Supplementary material 2).

3.5. Influence of position, period and other environmental variables on fish abundance

The mean variance of all eight fish groups examined, demonstrated the importance of distance from shore and position in driving patterns (Fig. 5). These two variables were also the most important in explaining the variability in fish abundance for most of the eight groups individually (Fig. 6).

Total fish abundance was significantly related to distance from shore, position, and period. There were more fish offshore than inshore and more fish in the second period (2013–2017) than in the first period (2002–2005). Fish abundance was significantly higher at offshore reefs than at mid submerged reefs, and mid-island reefs had significantly more fish than inshore reefs. However, mid-submerged reefs did not differ significantly from inshore reefs. The final model explained 84.7% of the variance observed in fish abundance. From this 84.7%, distance from shore explained 47%, position 45% and period 8%.

Labrid abundance was significantly related to position, distance from shore and period. There were more fish offshore than inshore and more fish in the second period (2013–2017) than in the first period (2002–2005). The final model explained 59.64% of the variance observed in Labrid abundance. From this 59.64%, position explained 48.5%, distance from shore 27.5%, and period 24%.

Pomacentrid abundance was significantly related to position, distance from shore, latitude and period. With more fish offshore than inshore, more fish in the second period (2013–2017) than in the first period (2002–2005), and more fish at lower latitudes (less at higher latitudes). Interestingly, the relationship between Pomacentrid abundance and distance from shore was complex, with more fish in mid reefs associated with islands than in inshore reefs, but less fish in mid submerged reefs than in inshore reefs. Offshore reefs had slightly lower

Table 2

PERMANOVA significance of groups for main factors of interest, interaction and pairwise comparison. In-off = inshore and offshore positions significantly differ. In = inshore, off = offshore. Bold = P (perm) significance level $\alpha < 0.05$. Light grey italics $\alpha > 0.25$.

Group	Subgroup	Position	Period	Year (period)	Position $\times$ period	Pairwise: position
Surrogate families	Labrids	0.0001	0.0078	<i>0.8000</i>	0.0023	All differ
	Pomacentrids	0.0001	0.005	<i>0.157</i>	0.0013	All differ
	Chaetodontids	0.0001	<i>0.2312</i>	0.0368	<i>0.2336</i>	In-off
Ecoregions	Tropical spp.	0.0001	0.0007	<i>0.2574</i>	0.0004	All differ
	Subtropical spp.	0.0001	0.0357	0.0316	<i>0.6743</i>	All differ
	Temperate spp.	0.0001	0.0421	<i>0.0586</i>	0.0473	All differ
Endemics	SW Pacific subtropical endemics	0.0001	<i>0.0656</i>	0.0264	<i>0.6848</i>	All differ
Trophic groups	Higher carnivores	0.0001	0.0282	<i>0.0617</i>	<i>0.0714</i>	All differ
	Invertivores	0.0001	0.0034	<i>0.1714</i>	0.0326	In-off
	Herbivores	0.0001	0.0345	<i>0.1412</i>	0.0178	All differ
	Planktivores	0.0001	0.0264	<i>0.2118</i>	0.0115	All differ

Pomacentrid abundance than inshore reefs, but the difference was not statistically significant (0.088). Still distance from shore was positively and significantly related to overall Pomacentrid abundance. The final model explained 74.5% of the variance observed in Pomacentrid abundance. From this 74.5%, position explained 46%, distance from shore 44%, latitude 8% and period 2%.

Chaetodontid abundance was significantly related to position and average annual temperature. There were more butterflyfish on offshore reefs than on mid-shelf reefs with similar abundance between mid-island and mid-submerged reefs. There was higher abundance on mid reefs than inshore reefs. Chaetodontid abundance significantly increased with average annual temperature. The final model explained 46.5% of the variance observed in Chaetodontid abundance. From this 46.5%, position explained 71% and average annual temperature 29%.

Tropical fish abundance was significantly related to the interaction between position and period. There were generally more fish in the second period (2013–2017) than in the first period (2002–2005) but this relationship was not significant. The interaction between position and period was significant, indicating that there were significantly more tropical fish in the second period but only in mid-submerged and offshore reefs, not in mid-island or inshore reefs. Tropical fish abundance was significantly higher offshore than inshore. The final model explained 91.03% of the variance observed in tropical abundance. From this 91.03%, position explained 54%, distance from shore 39%, period 5%, and the interaction between position and period explained 3%.

Subtropical abundance was significantly related to distance from shore and period. There were more fish offshore than inshore and more fish in the second period (2013–2017) than in the first period (2002–2005). The final model explained 41.5% of the variance observed in subtropical abundance. From this 41.5%, distance from shore explained 88%, and period 12%.

Temperate fish abundance was significantly related to distance from shore, to the interaction between position and period, to latitude, to average annual temperature, and to minimum depth. There were less temperate fish offshore than inshore. This was not a consistent inshore-offshore gradient as there were more temperate fish on mid reefs associated with islands than on inshore reefs, although this difference was not significant (0.08). There were more fish in the second period (2013–2017) than in the first period (2002–2005). There were more temperate fish as minimum depth increased, and as latitude increased. There were less temperate fish with higher annual average temperatures. The final model explained 49.4% of the variance observed in temperate fish abundance. From this 49.4%, position explained and distance from shore explained each 20%, the interaction between position and period explained 13%, average annual temperature 13%, latitude 13%, minimum depth 12%, and period 8%.

Abundance of subtropical species that are endemic to the southwest Pacific was significantly related to period and to distance from shore. Keeping average annual temperature and position improved model fit but these were not significantly related to fish abundance. There were

more fish offshore than inshore, and more fish in the second period (2013–2017) than in the first period (2002–2005). The final model explained 42.66% of the variance observed in the abundance of this group. From this 42.66%, distance from shore explained 44%, position 35%, period 10%, and average annual temperature 10%.

4. Discussion

Overall, strong cross shelf patterns have persisted over the duration of this study in this marine park. Although located in a climate change hot-spot (Last et al., 2011; Poloczanska et al., 2007) where changes in species and benthic habitat distributions have been reported (e.g. anemonefishes and host anemones, kelp) (Last et al., 2011; Malcolm and Scott, 2017; Vergés et al., 2016), the Habitat Classification System developed for the SIMP has maintained its validity as a coarse surrogate for biodiversity pattern over this 16 year time-frame. The HCS continues to broadly represent biodiversity and abundance patterns, at least for shallow (< 25 m depth) reef fish, with discrete assemblage clusters in each habitat category persisting between 2001 and 2017.

All four HCS position categories examined: inshore, mid island, mid fully submerged, offshore; significantly differed by overall assemblage, as well as for various trophic, ecoregion, endemic, and key family groups. These patterns are not driven by one or few groups overwhelming the others. The reef fish assemblage has remained more tropical-subtropical offshore, more temperate-subtropical inshore and temperate-subtropical-tropical on mid reefs throughout the study. From modelling, both position (categorical) and distance from the mainland coast (continuous), were the main drivers of the occurrence and abundance for the majority of groups. In the absence of a tested HCS elsewhere, distance from the coast (at least for a coastal MPA adjacent a boundary current) would be a good starting point for selecting an array of reefs to represent biodiversity and abundance patterns (Harrison and Smith, 2012; Hoey and Bellwood, 2008; Malcolm et al., 2012; Williams and Hatcher, 1983; Wismer et al., 2009). At the very least, a mix of reefs from inshore to the furthest offshore in a coastal MPA should be included in ‘no take’ areas as a MPA management strategy (Emslie et al., 2015; Magris et al., 2015; McCook et al., 2009), especially where multiple threats and risks to biodiversity have been identified from inshore to offshore (NSW Marine Estate Management Authority, 2015).

Period, or its interaction with position, also influenced all groups except for Chaetodontids, with greater abundance in all cases in the second period (2013 to 2017). Overall there has been an increase in abundance of reef fish in the SIMP over time. This could be partly influenced by overall increasing abundance through time associated with longer duration of MPA spatial management (i.e. 10 years in 1991, 26 years in 2017). Additionally or alternatively, an overall increase in abundance through time could be influenced by a ‘tropicalisation’ signal, especially given the temperate assemblage and subtropical endemic assemblage were negatively affected by sea temperature and the Chaetodontids were positively influenced.

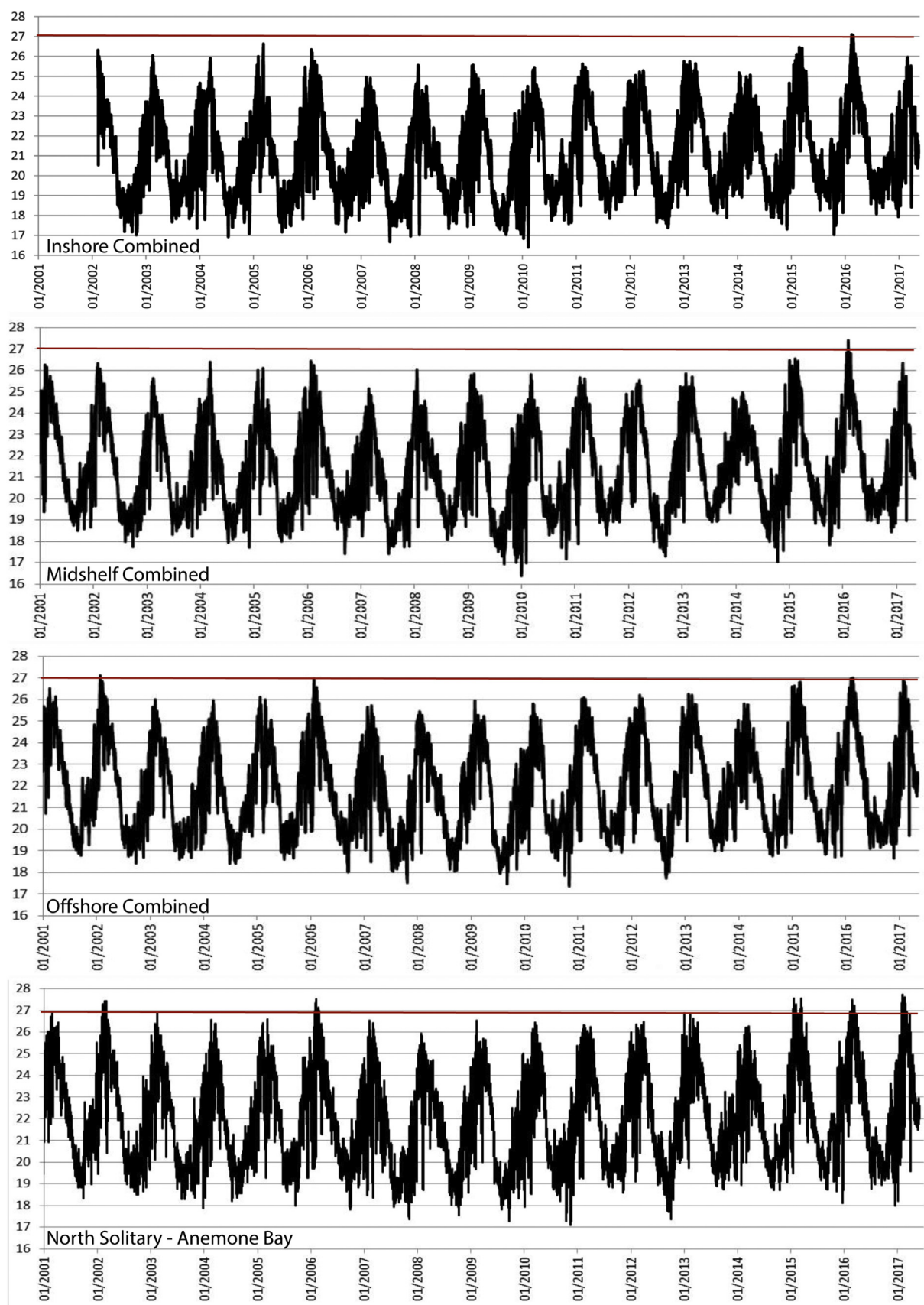


Fig. 4. In situ sea temperature patterns inshore mid (island) and offshore for 2001 to 2017, 30-minute records. Inshore (2 sites combined), mid islands (2 sites combined), offshore (North Solitary Island: 2 sites combined). Red lines show 27 °C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Annual averages, minimums, maximum. Bold numbers denote the warmest and coldest temperatures recorded from 1,824,642 records. Grey shaded cells = years by position when 27 °C was exceeded. To access the full set of temperature data, refer SM 2.

Annual		2001	2003	2004	2005	2013	2015	2016	2017
Minima	Inshore	—	17.35	16.93	17.17	17.88	17.03	17.95	17.61
	Mid	18.5	18.22	17.72	17.99	18.90	17.83	18.44	18.08
	Offshore	18.77	18.60	18.40	18.59	18.97	18.71	18.64	18.20
	N.Sol	18.33	17.87	18.19	17.99	18.74	18.11	17.98	18.20
Maxima	Inshore	—	26.05	25.91	26.63	25.75	26.45	27.09	25.96
	Mid	26.27	25.65	26.40	26.12	25.86	26.56	27.40	26.35
	Offshore	26.5	26.02	25.98	26.13	26.27	26.82	27.01	26.90
	N.Sol	26.91	26.91	26.58	26.59	26.81	27.57	27.51	27.72
Average	Inshore	—	21.14	20.84	21.00	21.57	21.45	21.65	20.97
	Mid	21.88	21.38	21.23	21.48	21.81	21.71	21.88	21.33
	Offshore	22.31	21.66	21.61	22.05	22.21	22.25	22.17	21.96
	N.Sol	22.42	21.72	21.69	22.22	22.26	22.42	22.29	22.04

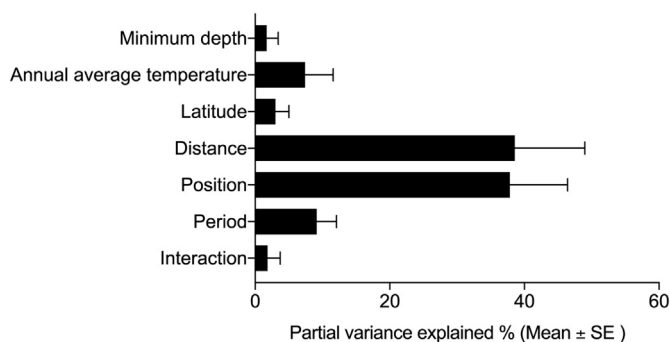


Fig. 5. Standardized partial coefficients indicate the mean of partial variance explained by each environmental variable across 8 fish functional groups. Distance from shore (quantitative) and position (qualitative) are the variables that explain most of the variability in fish abundance. Only significant variables are plotted, error bars denote standard error. Interaction = interaction between period and position.

Position separates the ‘mid distance from mainland coast’ category into ‘island’ and ‘fully submerged’ reef, which cluster together in

relation to inshore and offshore categories, but which are significantly different from each other. Mid-island reefs, with aspects protected from prevalent SE winter storm swell events, may have greater potential for a more coral-based tropical fauna than reefs fully exposed (Friedlander et al., 2003). Although, the greatest changes in assemblage pattern associated with ‘tropicalisation’ have occurred on fully submerged mid reefs, which over the study have become more similar (albeit still significantly different) to mid islands in terms of the reef fish assemblage being less temperate and more tropical in ecoregion affiliation. A separate study in the SIMP found an increase in tropical herbivores and a dramatic reduction in temperate kelp habitats on mid fully submerged reefs during the timeframe of this study (Vergés et al., 2016). Homogenisation of assemblages associated with climate change is a negative impact to biodiversity (Dornelas et al., 2014). In this region where assemblages of tropical, subtropical and temperate biota are juxtaposed, if there is a future reduction in this heterogeneity (i.e. homogenisation) associated with ‘tropicalisation’, this will reduce a key aspect of the biodiversity values in this MPA. However, even if reduced, the assemblage structure and composition in one habitat category cannot be represented within another while differences remain significant and therefore should be considered when spatially planning for conservation.

Increased frequency and intensity of perturbations such as major storms and coral bleaching events, related to climate change, may also cause changes in biodiversity patterns to occur more rapidly than decadal temporal scales in which MPA management plans are often in place (Magris et al., 2015). Other components of biodiversity such as species occurrence and abundance certainly change at temporal scales much finer than decadal. Species shifts and range extensions are also occurring (Last et al., 2011) and dramatic changes in biotic habitat have been recorded at sub-decadal temporal scales (Wernberg et al., 2011). Some of these are due to direct effects from disturbances (Bridge et al., 2014; Ferrari et al., 2016; Wernberg et al., 2016) and others due to trophic cascades such as increased levels of herbivory (Vergés et al., 2014). In the SIMP, reef fish assemblage patterns persisted over the study duration even though there were some major disturbances, especially in the second period. This included an intense large swell event in 2009 as part of a destructive East Coast Low storm system (Vergés et al., 2016). There was also a widespread coral bleaching event throughout northern and eastern Australia (Hughes et al., 2017). Thus, although there are likely to be impacting events during the duration of a marine park management plan, our findings demonstrating persistence in spatial biodiversity and abundance patterns, support applicability of a well-designed representative management plan at a decadal temporal scale. Stability in temperate reef communities over decadal scales have also been demonstrated further south (Stuart-Smith et al., 2010). However, it is possible the effects of the 2016 coral bleaching event on these fish assemblage patterns are yet to be fully realised. In the case of a regionally extensive and catastrophic

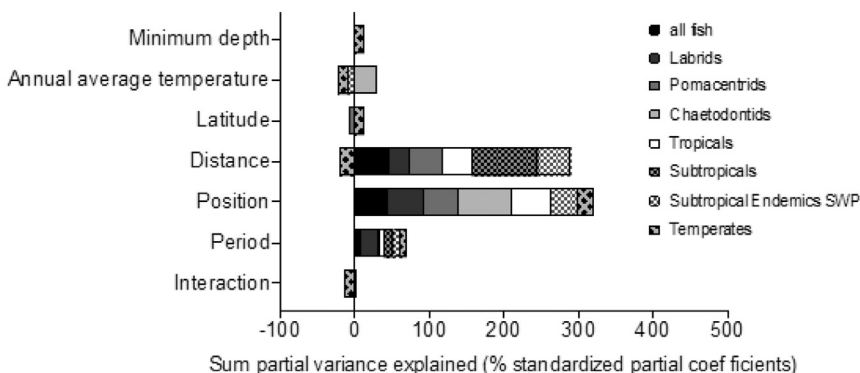


Fig. 6. Standardized partial coefficients indicate the mean of partial variance explained by each environmental variable and each fish functional groups. Distance from shore (quantitative) and position (qualitative) are the variables that explain most of the variability in fish abundance for all 8 functional groups explored in this study. Only significant variables are plotted. Interaction = interaction between period and position. Note that values on the left side of the zero line represent negative relationships, while values on the right positive relationships. The value along the x axis goes beyond 100 because these are summed values from the 8 functional groups.

ecosystem change, such as the 2011 marine heat-wave event in Western Australia (Bridge et al., 2014; Ferrari et al., 2016; Wernberg et al., 2016), patterns will likely change and a re-evaluation of spatial management arrangements may be required.

Acute disturbances are spatially variable within and among categories in a habitat classification system, as discussed. Given this variability, strategies which build spatial and temporal resilience into marine park design should be incorporated when utilising a coarse HCS to help plan spatial arrangements for MPA biodiversity representation. These include replicating multiple examples of biotypes within each HCS habitat category to spread risk and provide insurance against impacts and perturbations (McCook et al., 2009). Additionally, resilience may also be enhanced by taking a precautionary approach to maximise the spatial extent protected within ‘no take’ area (Sala and Giakoumi, 2017), and within each habitat category, to increase representation and connectivity (Makino et al., 2014; McCook et al., 2009). Resilience may also be improved by finer scale spatial mapping approaches (e.g. predictive modelling) that are complementary to the HCS approach, to help inform selection of ‘no take’ candidate reefs within an HCS category. Finer scale strategies will be particularly insightful within HCS categories undergoing the strongest assemblage shifts (i.e. mid fully submerged reef category in the SIMP). A complementarity approach to select reefs that are most dissimilar within that HCS category (e.g. using a systematic tool such as Marxan combined with species distribution modelling) (Ferrari et al., 2018a) will enhance the opportunity to maintain heterogeneity and regional (gamma) diversity compared to reefs that are more similar.

The strength of oceanographic and physical features has helped to maintain the assemblage patterns represented by the HCS. This includes the coastal geomorphology and the EAC. As a western boundary current, the EAC maintains a strong cross-shelf gradient in northern NSW, even though the current is strengthening and penetrating further southwards (Ridgway, 2007) and is showing enhanced warming (Wu et al., 2012). From sea temperature thermistor logger records, 2016 was the first time 27 °C water was experienced at the inshore and mid sites. Yet averages were still higher offshore in that year, with the warmest maxima at the furthest offshore location (North Solitary Island) and the coolest minima inshore. Even with ongoing strengthening and ocean warming it is likely that there will remain separation between inshore and offshore in oceanographic patterns such as sea temperature. However, there may be unidirectional phase shifts in all biotic categories, with offshore increasingly tropical with proportionally fewer subtropical species and inshore decreasingly temperate with proportionally more subtropical species (i.e. inshore resembling mid-2002, and mid resembling offshore-2002).

Globally, sea temperature has a major effect on diversity patterns in marine ecosystems (Tittensor et al., 2010). From modelling, sea temperature itself generally did not drive group patterns at the spatio-temporal scale of our study, although there are distinct temperature patterns from inshore to offshore in relation to the EAC. Temperature was significant and important for three groups: temperates, subtropical endemics and chaetodontids, but not as important as position. Chaetodontid abundance did increase with warmer annual average temperatures, the opposite of temperate species which decreased, as could be expected for a dominantly tropical family. The highest abundance was in the latter part of period 2, when the warmest temperatures were recorded. However ‘warmer temperatures’ over time leading to increasing environmental suitability for this tropical-dominated family would likely be tempered, at least for some species, by increased impacts to corals through temperature stress, given the strong relationship of some Chaetodontids with scleractinian corals (Pratchett et al., 2006).

Two ‘special’ sites in the marine park maintained their unique assemblage characteristics over the study period. Both have been zoned ‘no take’ since the early nineties. ‘Fish Soup’ is named for being rich and abundant in high order predators. However, it is not full of predatory fish just because it is zoned ‘no take’. For example, elsewhere within the

SIMP, ‘no take’ zones do not have this abundance. Yet without this level of management protection, it is likely Fish Soup would have considerably lower abundance of targeted species (Babcock et al., 2010; Claudet et al., 2008; Lester et al., 2009; Malcolm et al., 2015). It is a result of ‘no take’ protection combined with an exceptional set of habitat, oceanography and connectivity characteristics. Decadal scale maintenance of unique biodiversity characteristics at these sites support planning mechanisms that identify and include ‘special’ sites no matter the overall planning approach used. Qualitative identification of special sites, identified by local knowledge holders, is crucial for representing unique biodiversity arrangements within an MPA (Ferrari et al., 2018a; Game et al., 2018; Mangubhai et al., 2015).

Where a multiple use MPA has a core objective of conserving biodiversity, those responsible for its management have to make planning decisions (i.e. develop spatial plans, draw lines on maps) irrespective of the extent of biodiversity knowledge and knowledge gaps within that MPA and ecological understanding. As spatial management plans are influenced by a wide variety of social, economic, political and ecological input, robust surrogates for biodiversity and abundance patterns will help managers make and defend informed decisions (Arafah-Dalmau et al., 2017). Although potential changes to biodiversity within the likely duration of a spatial plan need to be considered and should be incorporated (Magris et al., 2015), potential changes should not preclude using an existing and robust HCS. It is still worth planning for biodiversity representation at the decadal scale, using habitat classification approaches, even though changes occur. Our study findings strongly support this, given that position was always more important than period or temperature, indicating the HCS used in the SIMP is currently robust to time and climate change. However, a representative habitat classification approach is not a stand-alone planning tool but should be used in conjunction with other approaches, such as species distribution models and local expert knowledge, to better inform successful planning.

5. Conclusions

Habitat surrogacy has continued application for marine spatial planning even in the face of climate change, and at a coarse level is robust to future changes at the decadal scale (Pech et al., 2017). Where there are strong environmental or physical features that are driving patterns, the continuation of those features will likewise drive persistence in biotic pattern. However, a more precautionary approach with increased replication of ‘no take’ areas within HCS categories where greatest shifts have been recorded, will improve the likelihood of biodiversity representation, particularly if finer-scale studies (e.g. predictive modelling) and systematic approaches to spatial planning (e.g. Marxan) are undertaken (McCook et al., 2009). Likewise, locally known ‘special’ sites are likely to remain special and are desirable inclusions to highly protected areas aiming to conserve biodiversity (Ferrari et al., 2018a).

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